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THE SKEWNESS OF THE THORAX IN THE ODONATA.

By James G. Needham and Maude H. Anthony.

(Plate VIII.)

Any one looking carefully at a dragonfly sees that the legs are attached far forward and the wings far back upon the thorax, and that the side plates of the latter are decidedly aslant. This arrangement of parts is an adaptation to perching on the sides of vertical stems without much alteration of the position maintained in flight. It makes for celerity in stopping and starting again. The legs are thrown forward where they readily reach and grasp the vertical stem, and the wings are shifted backward and tilted so that their cutting edges are directed obliquely upward, in which position a simple sculling action lifts the body instantly from its support.

In the jumping Orthoptera exactly the reverse inclination of the lateral thoracic sclerites has taken place: the legs have been shifted backward — especially the large hind ones used in jumping — and the side pieces are aslant with the opposite inclination. Doubtless these lateral sclerites (episternum and epimeron) were primitively placed at right angles to the axis of the body, so that the sutures between them were vertical, as they still are when first developed in dragonfly and grasshopper alike.

Among the orders the Odonata are extremely isolated, and, in their own way, undoubtedly highly specialized. As marks of their isolation the accessory genitalia of the males developed in an isolated position on the ventral side of the second abdominal segment, the type of venation, and the remarkable structure of the labium — especially, of the nymphal labium — have been frequently noted. But this skewness of the thorax, hitherto almost unstudied, is the external evidence of the most profound alterations of the whole bodily organization. As for the skeleton, the legs have moved forward and the wings backward, greatly increasing the areas between the sternum of the metathorax and the abdomen, and between the tergum of the mesothorax and the prothorax respectively, and these areas have been overgrown by neighboring lateral sclerites (mesepisternum in front and metepimeron behind). The unusual proportions and the new (dorsal and ventral) positions thus attained by these sclerites were long a puzzle to many eminent entomologists. The question of their homologies was finally set at rest by a study of the segmental muscles and sutures made by Dr. Calvert for his well-known catalogue, published in 1893. He showed that the muscles have retained fully their segmental arrangement, the wing muscles becoming enormously enlarged and taking on the general inclination of the thorax. The mid-lateral suture is completely and the others are almost obliterated.

This fusion of sclerites is doubtless an accompaniment of the increasing power of the wing muscles. The skeleton is further strengthened by the development of a unique system of carinæ, the strongest of which is the mid-dorsal thoracic carina, formed at the junction of the mesepisterna along the dorsal line, forking above and ending in an antealar crest, ending below in a transverse collar-like ridge abutting against the prothorax. There are also carinæ along the upper ends of the lateral sclerites about the wing bases, and others trussing the floor of the metathorax between the bases of the hind legs and the abdomen. Doubtless these all contribute to the strength of the thoracic skeleton, and enable it to withstand the pull of the enormously large and powerful wing muscles. If in a dragonfly that has newly emerged from the nymphal skin and that has not yet had time for the hardening of the skeleton, the muscles be stimulated artificially to contract (as by putting in alcohol or cyanide bottle) they draw the thorax into a crumpled and contorted condition. Doubtless a careful study of this system of carinæ, and of the external topography of the thoracic skeleton in general would yield good results: but it is a less ambitious undertaking that this paper records.

Impressed by the differences in degree of skewness in the thorax of a number of dragonflies that were lying before him one day, the senior author bethought himself that this skewness might be measured, and devised as an instrument for the purpose the goniometer shown in Pl. VIII, Fig. 1. This was constructed with little trouble out of a discarded box top, about 100 mm. square, a small brass protractor scale, a bicycle spoke, and a piece of brass about 25 mm. square. The brass was first drilled through the center and reamed out so that the head of the bicycle spoke would fit it neatly and rotate in it smoothly. Then the corners of the brass were drilled to receive screws. Then, with the spoke in place, its head flush with the surface of the brass, the latter was screwed fast to the under side of the wooden base, nearer the hinge edge of the cover, from which the side strip that was underneath had been removed. Thus the spoke was securely held by its head while free to rotate in the brass. Then the spoke was bent twice at right angles in an elongate **U** with unequal arms, the first bend perpendicular to, the second parallel to the surface of the board, the two arms being strictly parallel and far enough apart to allow the placing of the body of the largest dragonfly between the upper arm and the wooden base (Pl. VIII, Fig. 1). Then the protractor scale was glued to the wooden base in such position that its center of curvature was exactly over the center of the pivot below the base. The longer upper arm of the **U** then crossed the center in any position of rotation, and its end crossing the scale served as an indicator.

To use this goniometer a dragonfly with wings folded back to back was laid on a broad glass slip (this merely for convenience in moving the specimen) and brought to rest with its predetermined base line of angle measurement coinciding with the base line of the protractor scale. Then the index arm above was moved parallel with the suture forming the other limb of the angle to be measured. Then the angle was read by sighting along the edge of the indicator, keeping the exact center and the degree to be read in alignment. Thus the three successive operations — the placing of the specimen, the adjustment of the indicator and the reading of the scale — were done independently and in the order stated. This made for accuracy, but there were both mechanical and anatomical reasons why great accuracy was unattainable.

1. *Mechanical.* — The base line was too short. It was impossible to go beyond the confines of the combined meso- and metathorax and have fixed points, owing to the flexibility of the articulations with prothorax and with abdomen. To settle upon two points that should

determine a longitudinal line in comparison with which the angle of inclination of the sclerites should be measured was not easy. After canvassing the external topography of the thorax carefully, we settled upon the pleural articulation of the middle coxa for the anterior point (Pl. VIII, Fig. 2, *b*) and the infero-lateral articulation of the thorax and abdomen for the posterior, the two determining the base line *bd* of Fig. 2. By comparing Fig. 1 * it will be seen that the two points are so close together as to occasion difficulty in bringing them into exact coincidence with the base line of the scale.

2. *Anatomical.* — The anatomical sources of error were several. (*a*) The articulations used to determine the base line are something more than points in breadth. (*b*) They are sometimes obscured by hairs. (*c*) The sutures with which the indicator must be made parallel are sometimes sinuous, and their general direction has to be estimated.

At first the skewness of the three lateral sutures and of the dorsal carina were measured, but as the differences discovered were rather less than the rather wide limits of probable error, only the first lateral (humeral) suture was measured to the end, and that and the tilt of the wing bases in the opposite direction are reported upon below.

The diagrammatized photograph (Fig. 2) shows these angles: *abc* is the angle made by the humeral suture *cb* with the perpendicular *ab* to the base line *db*, assumed to be parallel with the axis of the body. This angle measured upon the arc *x* represents the degree of skewness or inclination of that suture.

cdb is the angle made by a line *cd* drawn through the wing bases with the base line *bd*, and is measured upon the arc *z*. The wing bases are assumed to have rested primitively upon the line *ec* parallel to *db*. The specimen shown in Fig. 1 is nearly in position for measuring this angle.

The actual measurements were all made by the junior author upon miscellaneous papered specimens. Each specimen selected was measured first upon one side and then upon the other, and after intervening measurement of other species, was measured again, and then the average of all the measurements was taken. But one specimen was used for each species and the sex was disregarded. Some of the first meas-

* The specimen is off the base line in Fig. 1, having slipped out of place just before this photograph was taken.

urements made showed considerable discrepancies and were discarded altogether; but, with practice, they came into much closer agreement. It is not claimed, however, that the figures herein given are to be relied upon absolutely within the limits of two or three degrees.

Suborder **Anisoptera.**

Fam. ÆSCHNIDÆ.

ÆSCHNINÆ.

	x	z		x	z
Boyeria irene	21	19*	*Staurophlebia magnifica*	36	25
Anax junius	27	21	*Epiæschna heros*	37	23
Æschna californica	34	22	*Gomphæschna furcillata*	37	24
Coryphæschna ingens	34	25	*Gynacantha trifida*	39	27
Æschnophlebia anisoptera	35	34†	*Basiæschna janata*	42	27
Æschna verticalis	36	23	*Planæschna multipunctata*	42	28

GOMPHINÆ.

Dromogomphus spinosus	31	25	*Lanthus albistylus*	42	28
Gomphus simillimus	32	22	*Herpetogomphus designatus*	41	28
Gomphus villosipes	33	26	*Ophiogomphus serpentinus*	44	27
Gomphoides stigmatus	36	26	*Progomphus obscurus*	44	27
Gomphidia confluens	37	26	*Onychogomphus uncatus*	47	27
Aphylla producta	39	27	*Epigomphus paludosus*	47	29
Hagenius brevistylus	40	22*	*Hemigomphus ochraceus*	50	29†
Gomphus dilatatus	41	22			

PETALURINÆ.

Tachopteryx thoreyi	40	28

CORDULEGASTERINÆ.

Cordulegaster diastatops	37	35

Fam. LIBELLULIDÆ.

MACROMIINÆ.

Didymops transversa	29	20	*Epophthalmia elegans*	33	18*
Macromia magnifica	32	22	*Synthemis brevistyla*	39	33†

* Minima: second column.

† Maxima: second column.

CORDULIINÆ.

Helocordulia uhleri	30	25	*Tetragoneuria canis*	36	29†
Epicordulia princeps	33	24	*Cordulia shurtleffi*	37	24
Hemicordulia tau	34	23*	*Somatochlora elongata*	38	24

LIBELLULINÆ.

Perithemis domitia	28	21	*Mesothemis simplicicollis*	43	34
Acisoma panorpoides	28	24	*Trithemis minuscula*	43	38*
Rhyothemis splendida	33	25	*Brachythemis contaminata*	44	26
Onychothemis abnormis	31	22	*Tramea carolina*	44	27
Brechmorhoga mendax	34	24	*Pachydiplax longipennis*	44	27
Lepthemis vesiculosa	34	27	*Crocothemis erythræa*	44	30
Belonia herculea	35	19*	*Anatya anomala*	45	29
Diastatops tincta	36	27	*Neurothemis equestris*	45	31
Zygonyx iris	36	28	*Micrathyria didyma*	47	27
Dythemis velox	37	29	*Potamothemis americana*	46	29
Orthetrum albistylum	38	25	*Sympetrum rubicundulum*	46	31
Miathyria marcella	39	24	*Pantala flavescens*	47	25
Plathemis lydia	40	22	*Celithemis elisa*	48	30
Ladona julia	40	28	*Palpopleura vestita*	49	24
Libellula pulchella	41	23	*Melamarptis minekii*	49	31
Orthemis ferruginea	41	27	*Leucorhinia glacialis*	51	23
Nannothemis bella	42	32	*Macrothemis* sp.‡	52	30
Pseudophlebia minima	43	28			

Suborder **Zygoptera.**

Fam. CALOPTERYGIDÆ.

EPIOPHLEBINÆ. ‡

Epipophlebia superstes	43	45

EPALLAGINÆ.

Euphæa decorata	51	45*	*Anisopleura lestoides*	64	54
Rhinocypha	63	61†	*Bayadera indica*	67	57
Diphlebia lestoides	64	53			

* Minima : second column.

† Maxima : second column.

‡ An undetermined species from Brazil, selected for the extreme reduction of its venation.

§ The preoccupied Selysian name *Palæophlebia* being now replaced by *Epiophlebia* (Calvert, Ent. News, vol. XIV, p. 208, 1903), the subfamily name is here modified to correspond.

VESTALINÆ.

Neurobasis chinensis	46	39	*Calopteryx maculata*	54	43
Mnais strigata	50	40	*Hetærina americana*	58	40
Calopteryx angustipennis	51	35*	*Lais pudica*	59	49†

THORINÆ.

Thore picta	52	48	*Cora inca*	59	50

Fam. AGRIONIDÆ.

LESTINÆ.

Archilestes grandis	59	38	*Lestes rectangularis*	66	48

AGRIONINÆ.

Calicnemis atkinsoni	57	51	*Disparoneura vittata*	64	55
Hyponeura lugens	58	53	*Oxyagrion terminale*	64	58
Platycnemis pennipes	61	42	*Nehallennia irene*	64	61
Hemicnemis bilineata	61	51	*Leptagrion macrurum*	65	47
Amphiagrion saucium	62	42*	*Enallagma doubledayi*	65	48
Xanthagrion erythroneurum	62	47	*Protoneura capillaris*	65	53
Ischnura grællsii	62	48	*Telebasis allaudi*	65	53
Argia violacea	63	59	*Ceriagrion glabrum*	65	53
Ceratura capreola	64	48	*Acanthagrion gracile*	65	54
Mecistogaster sp ?	64	49	*Acanthagrion cheliferum*	65	57
Anomalagrion hastatum	64	51	*Erythragrion salvum*	67	45
Agriocnemis pulverulans	64	55	*Aciagrion pallidum*	72	62*

The maxima, minima and averages for both angles are given for the subfamilies, of which representatives were studied, in the following table:

			Angle of humeral suture.			Angle of tilt of wing bases.		
			Mi.	Ma.	Av.	Mi.	Ma.	Av.
Anisoptera	ÆSCHNIDÆ	ÆSCHNINÆ	21	42	35	19	34	25
		GOMPHINÆ	31	50	40	22	29	26
		PETALURINÆ	40	—	—	35	—	—
		CORDULEGASTERINÆ	37	—	—	35	—	—
	LIBELLULIDÆ	MACROMIINÆ	29	39	33	18	33	24
		CORDULINÆ	30	38	35	23	29	25
		LIBELLULINÆ	28	52	41	19	38	30

* Minima: second column.

† Maxima: second column.

			Angle of humeral suture.			Angle of tilt of wing bases.		
			Mi.	Ma.	Av.	Mi	Ma.	Av.
Zygoptera	CALOPTERYGIDÆ	EPIOPHLEBIINÆ*	43	—	—	45	—	—
		EPALLAGINÆ	51	67	62	45	61	54
		VESTALINÆ	46	59	54	35	49	41
		THORINÆ	52	59	55	48	50	49
	AGRIONIDÆ	LESTINÆ	59	66	62	28	48	43
		AGRIONINÆ	54	72	62	42	62	49

The above listed material was the best selection that could be made from the material that happened to be at hand in the collection of the senior author. Only papered specimens could be used readily. Whole subfamilies are unrepresented, and the material used is insufficient to furnish a basis for true averages for any of the subfamilies. Yet notwithstanding this, and with all due allowance for error in the making of difficult measurements of angles, some general results are sufficiently evidenced by the figures obtained.

In the first place it is evident that the skewness of the thorax is much greater in the Zygoptera than in the Anisoptera, the average of the former being above the maximum of the latter. The minimum for both angles measured is found in the Æschninæ, and the maximum in the Agrioninæ. The widest range is shown by the Libellulinæ, and it is probable that this is due only in part to the selection of a wider range of representatives of this subfamily.

There was found less correlation between the two angles measured than might have been expected. It will be observed throughout that the maxima and minima rarely fall in the same places in the two columns. The angle that measures the inclination of the humeral suture is with a single exception greater than that measuring the tilt of the wing bases, *Epiophlebia* alone furnishing the reverse condition.

There is little correlation between the size of the insect and the inclination of the humeral suture : just how much, will be seen by glancing down the first column, which in each subfamily is arranged in accordance with the increasing angulation here. There appears to be much more correlation between mere size and the tilt of the wing bases : for it will be noticed in each group that the minimum falls upon one of the largest and the maximum on one of the smallest species.

It must not be forgotten for a moment that these measurements take no account of possible parallelisms within the subfamilies, nor of divergent lines of development, but give merely the degree of progress in two particular lines of specialization arbitrarily selected. The figures, however, are interesting to one who knows these species by sight — even surprising — especially in the Libellulinæ, where they seem to support no one's theory of the interrelationships of the genera.

PHRYGANIDIA CALIFORNICA, *PACKARD.*

By Beverly Letcher.

Had the general excellence of the account of the life history of this moth as set forth by Vernon L. Kellogg and F. J. Jack (Proceedings of the California Academy of Sciences, second series, Vol. V, 1895, page 562) been maintained throughout their article, there would hardly have been occasion for the present but with them critical observation seems to have ceased with the pupal stage. Other differences are slight but as they are of some interest, may be noted.

To afford a ready comparison of the head measurements, they have been tabulated, those of Kellogg and Jack appearing in the first column and those of the writer in the third. Little value can be attached to the several durations of stages in the fourth column as they were made on larvæ subject to the artificial surroundings of the study: they are from observations of the summer brood while those of Messrs. Kellogg and Jack were made on wintering larvæ.

Stage.	Kellogg and Jack.		Letcher.	
	Mm.	Days.	Mm.	Days.
Egg		10		10
1st	.68	14	.53, .67	8
" supplementary			.73	8
2d	1.14	13	1.15	6, 8
3d	1.45	17	1.32, 1.47	7
4th	1.88	25	1.82	8
5th	2.21	21	2.20	5
6th	2.57	12	2.31	9
Pupa		10		9

A practical agreement is to be noted for the 1st, 2d, 3d, 4th and 5th stages. My observations show a stage supplemental to the 1st and